A MID-TERTIARY FOSSIL FLOWER OF *SWIETENIA* (MELIACEAE) IN DOMINICAN AMBER

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ABSTRACT

We report a further example of an amber-embedded flower representative of Mid-Tertiary tropical forests from the Caribbean island of Hispaniola. The new fossil species **Swietenia dominicensis** (Meliaceae) consists of a functionally staminate flower whose urceolate filament tube bears 10 deltate-acuminate appendages. Within the mouth of the tube are 10 sessile stamens alternating with the appendages. The slightly exserted style bears a conspicuous disc-shaped stigma the surface of which is obscurely 5–6 segmented and minutely pitted. The perianth combines ciliolate calyx lobes with glabrous-margined petals, unlike any of the 3 modern species of *Swietenia*. The glabrous petals, as well as the form of the calyx, distinguish this flower from the Mexican fossil species *Swietenia miocenica* described by Castañeda-Posadas and Cevallos-Ferriz (2007).

RESUMEN

Citamos otro ejemplo más de flor incluida en ámbar representativa de los bosques tropicales del Terciario medio de la isla caribeña la Hispaniola. La nueva especie fósil **Swietenia dominicensis** (Meliaceae) consiste en una flor funcionalmente estaminada cuyo tubo urceolado lleva 10 apéndices deltado-acuminados. En la boca del tubo están 10 estambres sésiles alternando con los apéndices. El estilo ligeramente exerto lleva un estigma en forma de disco cuya superficie está oscuramente dividida en 5–6 segmentos y punteada diminutamente. El perianto combina lóbulos del cáliz ciliolados con pétalos glabros en los márgenes, a diferencia de las 3 especies modernas de *Swietenia*. Los pétalos glabros, así como la forma del cáliz, distinguen esta flor de la especie fósil mexicana *Swietenia miocenica* descrita por Castañeda-Posadas y Cevallos-Ferriz (2007).

INTRODUCTION

The flower described here as *Swietenia dominicensis* was illustrated incidentally by Poinar and Poinar (1999, p.19) in their book reconstructing the Late Oligocene-Early Miocene tropical forests of Hispaniola. It supplements the 9 species of fossil flowers thus far reported from amber mines in the Dominican Republic. The other described species of amber-embedded flowers are in the genera *Hymenaea* (Fabaceae) (Poinar 1991), *Trithrinax*, *Paleoraphe*, and *Roystonea* (Arecaceae) (Poinar 2002a, 2002b), *Licania* (Chrysobalanaceae) (Poinar et al. 2008a, revised by Chambers & Poinar 2010), *Persea* (Lauraceae) (Chambers et al. 2011a), *Trichilia* (Meliaceae, 2 species) (Chambers et al. 2011b), and *Trochanthera* (possibly Moraceae) (Poinar et al. 2008b). The flower of *Swietenia dominicensis* is similar in most respects to the 3 extant species of the genus (Styles 1981) and to *Swietenia miocenica* described from Mexican amber by Castañeda-Posadas and Cevallos-Ferriz (2007). Its distinguishing morphological trait is the combination of ciliolate calyx lobes with glabrous-margined petals, the other taxa having either the calyx and petals both ciliolate, or all perianth parts glabrous-margined. This minor difference is important in the taxonomy of the genus, although its usefulness in classification was questioned by Miller (1990, p. 479), who, however, misinterpreted the species differences as given by Styles (1981, p. 391). Other features, such as size of leaflets and petiolules, seed color, and capsule size, cannot be characterized for the fossil species. *Swietenia miocenica* was reported to have a calyx of 5 free lobes, whereas the species at hand, as well all living members of the genus, have a calyx "5-lobed to about the middle" (Styles 1981, p. 389).

MATERIALS AND METHODS

Like the several fossil species from the Dominican Republic cited above, the flowers originated from amber mines in the Cordillera Septentrional, between the cities of Puerto Plata and Santiago. The age of these deposits

has proven to be controversial, the oldest proposal being 45–30 mybp, based on coccoliths (Cépek in Schlee 1999) and the youngest being 20–15 mybp, based on foraminifera (Iturralde-Vinent & MacPhee 1996). The amber is principally deposited in turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994).

DESCRIPTION

Swietenia dominicensis K.L. Chambers & Poinar, sp. nov. (**Figs. 1–3**). TYPE: HISPANIOLA. DOMINICAN REPUBLIC: amber mine in the northern mountain range (Cordillera Septentrional), 1995, *unknown amber miner s.n.* (HOLOTYPE: catalogue number Sd-9-7, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Flower putatively staminate, total length (pedicel apex to tip of filament tube appendages) 3.85 mm, calyx shallowly cupulate (Fig. 2), ca. 1.0 mm long, fused portion 0.54 mm long, lobes 0.45 mm long, broadly rounded, spreading, margins ciliolate, petals 5, free, ca. 4.5 mm long, 2.2 mm at widest part, spreading or reflexed, somewhat contorted, elliptic to oblanceolate, obtuse, glabrous (including margins), filament tube urceolate (Fig. 1), glabrous, 2.9 mm long excluding appendages, 2.9 mm wide, appendages 10, deltoid-acuminate, ca. 0.8 mm long, slightly spreading, anthers 10, sessile, alternating with appendages, ca. 0.6 mm long (only a few visible for measurement), dehisced, hypothesized to be fertile, pistil present, ovary not visible, style exserted from filament tube, barely exceeding appendages, stigma enlarged, disc-shaped, 1.3 mm in diameter, densely minutely pitted, obscurely marked into 5–6 fused segments (Fig. 3).

Etymology.—From the amber's source in the Dominican Republic.

DISCUSSION

We hypothesize that the flower is staminate in function, although its anthers are dehisced and are not well enough displayed to be sure that pollen was produced. The flower's overall shape, including the position and morphology of the stigma, matches well the excellent drawings of staminate flowers of *Swietenia mahagoni* published by Miller (1990, p. 478). We also compared it with illustrations of the other modern species, *S. humilis* and *S. macrophylla*, in Styles (1981) and with the description and photographs of the Mexican fossil species, *S. miocenica*, in Castañeda-Posadas and Cevallos-Ferriz (2007). Together with the examination of herbarium material of *S. mahagoni*, these references support our judgment that the Dominican fossil is best placed in *Swietenia*.

As noted by Styles (1981) and other authors (e.g. Helgason et al. 1996), the 3 modern species of the genus are "poorly defined biologically," are largely allopatric at the present time, and are "reasonably distinct morphologically" (Styles 1981). Putative hybrids, from the natural zones of contact in Costa Rica and Guatemala involving *S. humilis* and *S. macrophylla*, are intermediate for both ecological tolerance and morphological characters such as rachis length and leaflet size (Whitmore & Hinojosa 1977; Helgason et al. 1996). An extensive polyploid series of chromosome numbers is reported for the genus (Khosla & Styles 1975; Helgason et al. 1996). A further complication is that *S. mahagoni*, in particular, has been widely planted outside its original range in southern Florida and the larger Caribbean islands, thereby increasing the occurrences of species sympatry. The key distinction that we relied on to separate the present fossil from all other species is its combination of a ciliolate calyx with glabrous-margined petals. *Swietenia mahagoni* is described as having glabrous calyx lobes and petals, while the other 2 species under discussion have ciliolate petals and calyx (Styles 1981). Miller's remark (1990, p. 479) that "this distinction was not apparent in numerous specimens … that I studied" is offset by his statement, perhaps in error, that the calyx and corolla are ciliolate in *S. mahagoni* and smooth-margined in the other 2 species. Nonetheless, the differences in perianth pubescence described by Styles (op. cit.) have held true in practice (Pennington, pers. obs.).

Castañeda-Posadas and Cevallos-Ferriz (2007) differentiated *Swietenia miocenica* from this Dominican fossil, which they saw illustrated, but not described, in Poinar and Poinar (1999), by differences in the shape of the filament tube and petals. In addition, they described *S. miocenica* as having "a free calyx composed of five. … rounded lobes …," which would differentiate it from all other known species of the genus. To their species characterization we have added the lack of petal ciliolation in *S. dominicensis* versus its presence in *S. miocenica*. The age of *S. miocenica* given by these authors (Late Oligocene-Early Miocene, 26.0–22.3 mybp) approxi-

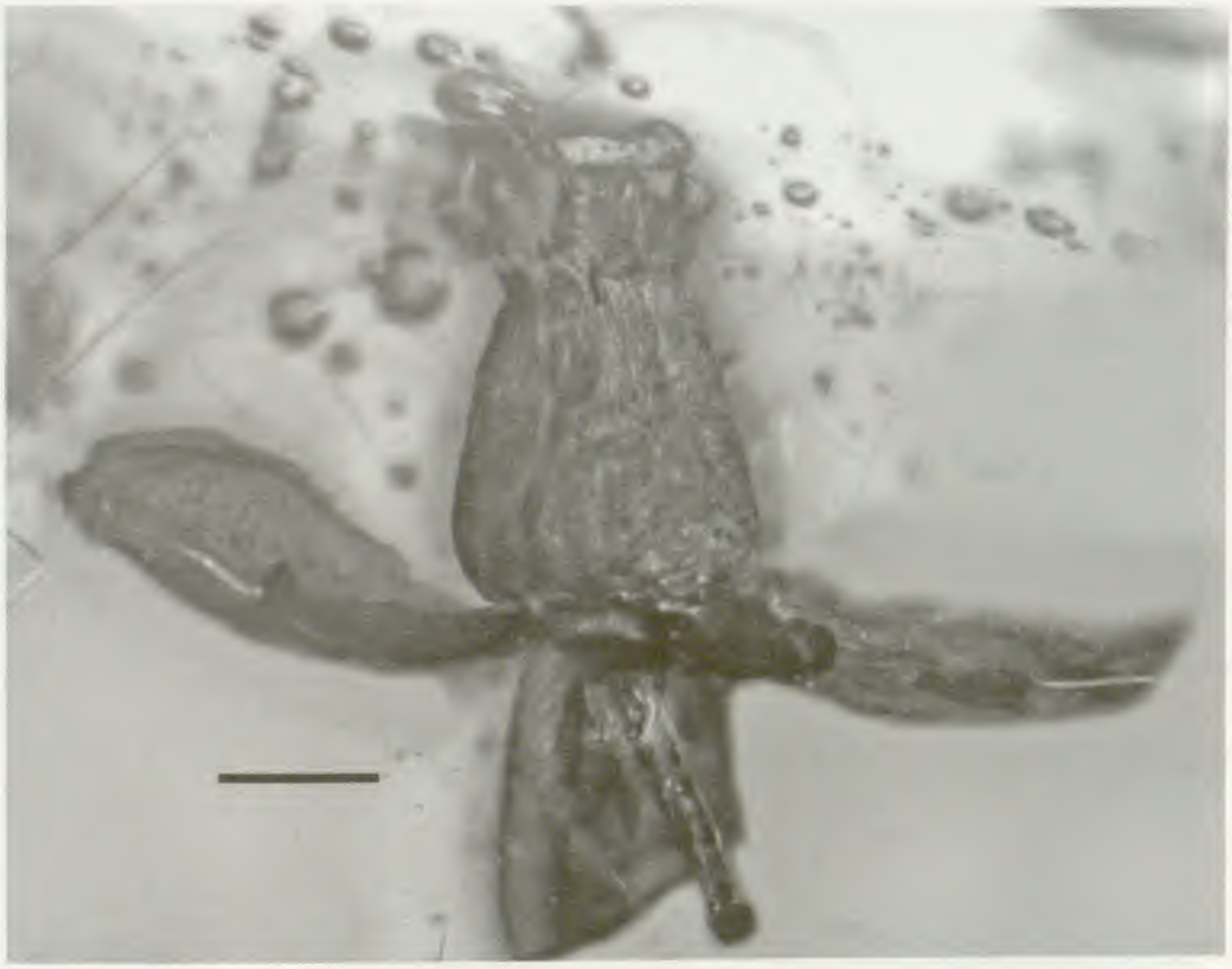

Fig. 1. *Swietenia dominicensis*. Flower in lateral view, showing anther tube with acuminate distal lobes, slightly exserted style, and capitate, discoid stigma. Black ovals on 2 petals are air bubbles. Scale bar = 1.5 mm.

Fig. 2. *Swietenia dominicensis*. Basal view of flower with pedicel in center. Arrows indicate 2 of 3 sepal lobes in focus. Sepal lobes ciliolate-margined, petals glabrous-margined. Scale bar = 0.45 mm.

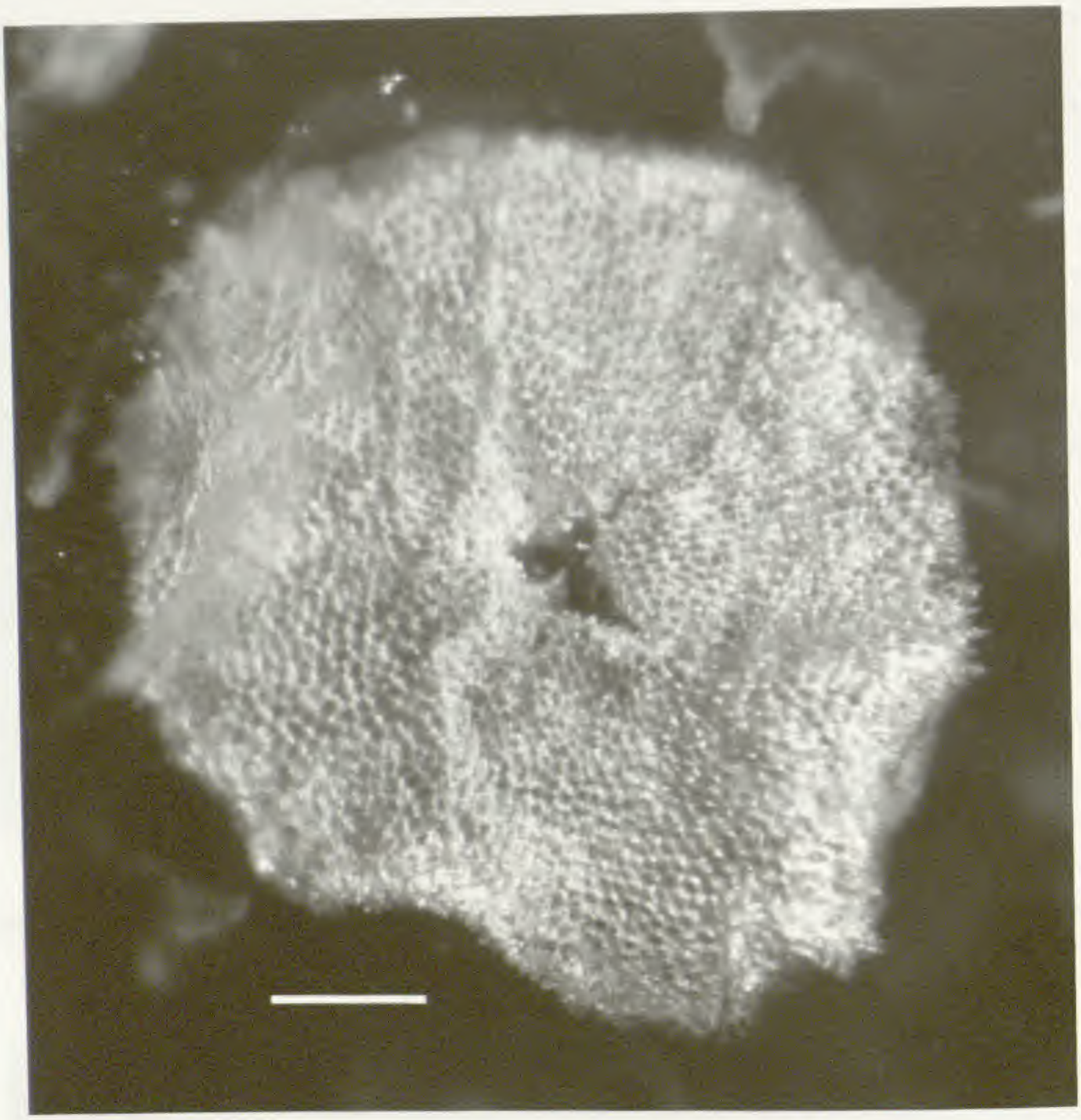

Fig. 3. *Swietenia dominicensis*. Stigmatic head of pistil. Note minute pores and irregular division into indistinct segments. Scale bar = 0.24 mm.

mates that of *S. dominicensis*. Nonetheless, we conclude that *S. dominicensis* is best described as a separate species, especially given the different provenance and the morphological details of calyx, filament tube, and perianth pubescence.

Swietenia is placed in the monophyletic subfamily Cedreloideae (formerly Swietenioideae) by Muellner et al. (2003, 2006). However, compared with the tribe Cedreleae, composed of *Cedrela* and *Toona* (Muellner et al. 2009), the remaining tribes Swietenieae and Xylocarpeae, as described by Pennington and Styles (1975), are not monophyletic (Muellner et al. 2003, 2006). *Capuronianthus* had previously been classified as a separate subfamily by Pennington and Styles (1975), but was later shown to be nested within Cedreloideae (Muellner et al. 2003). According to Muellner et al. (2003), "some genera and most tribes can only be diagnosed by using a combination of several characters." A well resolved and sufficiently supported molecular phylogenetic reconstruction including all genera of Cedreloideae (compare Muellner et al. 2011 for a recent test of more DNA markers in *Cedrela*, *Swietenia*, and other genera), along with a detailed morphological re-investigation, will ultimately lead to a new and robust tribal classification within Cedreloideae.

Muellner et al. (2006) discussed the fossil history of Meliaceae as a whole, with later reviews, in greater detail, for tribe Cedreleae (Muellner et al. 2009, 2010; Pennington & Muellner 2010). Fossils of Cedreleae have been reported from the Eocene and later periods, at both northern and mid-latitude sites in the Old and New Worlds. In proposing a West Gondwanan origin for family Meliaceae (Muellner et al. 2006), the authors discussed an "out-of-Africa" scenario, "with dispersal....[via] important routes across Eurasia and between Eurasia and North America provided by Beringia and the North Atlantic land bridge, and between North America and South America through island chains and/or direct land connections." A crown group age for *Swietenia* has

not yet been proposed. Based on fossil evidence (Europe, North America) and relaxed molecular clock dating, crown Cedreleae are believed to date back at least to the Early Eocene (Muellner et al. 2010; Pennington & Muellner 2010). The Late Oligocene-Early Miocene age of our fossil and that of Castañeda-Posadas and Cevallos-Ferriz (2007) verifies the Mid-Tertiary occurrence of *Swietenia* in Central and South America.

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